

# The functional and structural asymmetries of the superior temporal sulcus

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The superior temporal sulcus (STS) is an anatomical structure that increasingly interests researchers. This structure appears to receive multisensory input and is involved in several perceptual and cognitive core functions, such as speech perception, audiovisual integration, (biological) motion processing and theory of mind capacities. In addition, the superior temporal sulcus is not only one of the longest sulci of the brain, but it also shows marked functional and structural asymmetries, some of which have only been found in humans. To explore the functional-structural relationships of these asymmetries in more detail, this study combines functional and structural magnetic resonance imaging. Using a speech perception task, an audiovisual integration task, and a theory of mind task, this study again demonstrated an involvement of the STS in these processes, with an expected strong leftward asymmetry for the speech perception task. Furthermore, this study confirmed the earlier described, human-specific asymmetries, namely that the left STS is longer than the right STS and that the right STS is deeper than the left STS. However, this study did not find any relationship between these structural asymmetries and the detected brain activations or their functional asymmetries. This can, on the other hand, give further support to the notion that the structural asymmetry of the STS is not directly related to the functional asymmetry of the speech perception and the language system as a whole, but that it may have other causes and functions.

**Key words:** Superior temporal sulcus, asymmetry, speech perception, audiovisual integration, theory of mind, fMRI, anatomy.

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## INTRODUCTION

### Prolog

This article is about a putative “empty” space of the brain that has received growing interest over recent years – this article is about the superior temporal sulcus. The superior temporal sulcus (STS) is the structure of the temporal lobe that divides the superior temporal gyrus (STG) from the middle temporal gyrus (MTG). Consequently, the STS is one of the longest sulci of the brain and starts around the temporal pole and terminates at the angular gyrus in the inferior parietal lobe. Of course, this is not an “empty” space; talking about the STS means talking about the cortex in the depth of STS, hidden by the foldings of the STG and MTG.

This article also describes a personal history and how a research focus can evolve over the years. It all began with a study that asked a simple question: Which areas are more active when listening to speech sounds as compared to complex sounds and pure tones? The main difference was found in the middle part of left STS (Specht & Reul, 2003). The cortex in the depth of the STS responded significantly stronger to sounds that contained phonological information than to all other types of sounds. This result was in line with other reports at that time (Jäncke, Wüstenberg, Scheich, & Heinze, 2002) and these results were included in several review articles (Price, 2012; Price, Thierry & Griffiths, 2005; Scott, 2005). To further investigate possible transition effects between non-verbal and verbal sounds a new stimulus technique was applied, called “sound morphing” (Osnes, Hugdahl & Specht, 2011b; Osnes, Hugdahl, Hjelmervik & Specht, 2011a; Specht, Osnes & Hugdahl, 2009b; Specht, Rimol,

Reul & Hugdahl, 2005). In analogy to visual morphing sequencing, sounds were morphed from one category into another – from non-verbal into verbal sounds. Results from these studies showed, as expected, that the middle part of the left STS appeared to be very sensitive to the increasing presence of phonetic information. With the increase of activity that followed the manipulation of the morphed sounds, an increased leftward asymmetry was observed, suggesting that this part of the STS is very speech selective and shows the typical pattern of left-hemispheric speech dominance. Resulting from these findings, the STS became deservedly part of current models of speech perception (Hickok & Poeppel, 2007; Specht, 2014).

One could have been convinced by now that the middle part of the STS is an important – if not the most important – area in decoding phonetic information (Liebenthal, Desai, Ellingson, Ramachandran, Desai & Binder, 2010). However, initial doubts on this view occurred when comparing these consistent results with results from other studies, such as those on different variants of the Wisconsin Card Sorting Test, which do not contain any phonetic or auditory information but that have nonetheless activated regions within the STS (Lie, Specht, Marshall & Fink, 2006; Specht, Lie, Shah & Fink, 2009a). Although the STS was not the main focus of interest and finding in these studies, the results indicated a contribution from the STS (see Fig. 1). Emerging at the same time, there were an increasing number of reports identifying STS's important function in other cognitive processes as well. Consequently, Grit Hein and Robert T. Knight asked the following question in their seminal review: “Superior temporal sulcus – it's my area: Or is it?” (Hein & Knight, 2008).

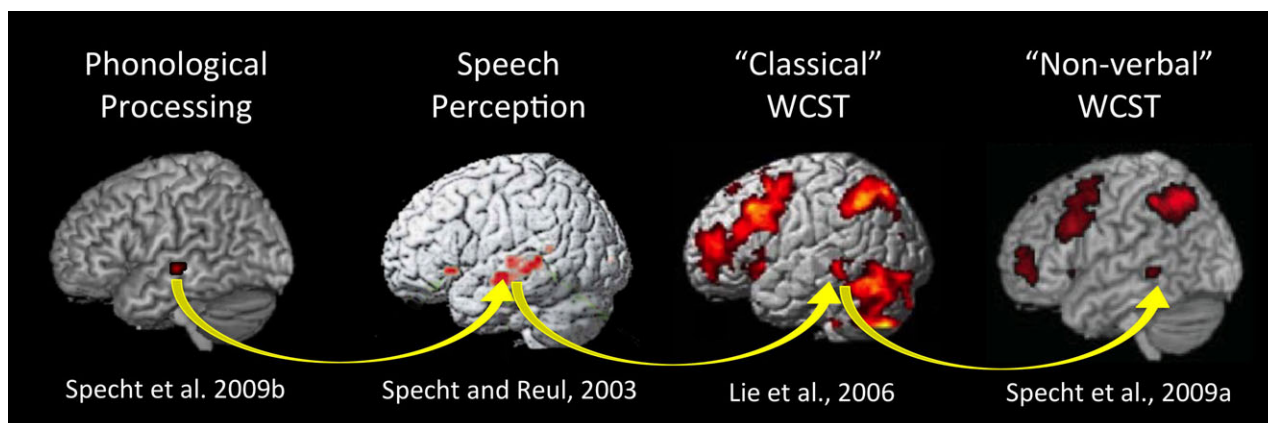


Fig. 1. Four different, unrelated studies, jointly showing a contribution of the superior temporal sulcus: From left to right: (1) The response to the parametric modulation of phonological information in a sound-morphing paradigm; (2) Brain response to real words in a passive listening condition, when brain response to complex non-verbal sounds are subtracted; (3) Brain response during the performance of a Wisconsin Card Sorting Test (WCST) with the “classical” – easy to verbalise items, like “three green squares”; and (4) WCST with items that are difficult to verbalise. [Colour figure can be viewed at [wileyonlinelibrary.com](http://wileyonlinelibrary.com)]

“Apparently, it is!” and therefore this study has been conducted.

#### Neuroanatomy of the STS

As mentioned, the STS is one of the longest sulci of the brain, running parallel and inferior to the lateral fissure. At its posterior point, it transverses the angular gyrus at the intersection to the inferior parietal lobe, with some inter-subject variability at its posterior end, called the caudal rami (Segal & Petrides, 2012). This follows as the main section of the sulcus within the temporal lobe also varies between subjects. In this region, inter-subject variability occurs in the frequency of sulcal pits and in the presence, absence, or size of superficial gyri, called “*plis de passage*,” that are connections between the superior and middle temporal gyrus, intersecting the STS (Im, Jo, Mangin, Evans, Kim & Lee, 2010; Leroy *et al.*, 2015; Ochiai, Grimault, Scavarda *et al.*, 2004).

More importantly, however, the STS shows a systematic double asymmetry between the left and right hemisphere: The STS is longer on the left but deeper on the right hemisphere (Leroy *et al.*, 2015). Furthermore, and more important for this report, this asymmetry is present only in humans (Leroy *et al.*, 2015). It is postulated that this asymmetry is genetically coded, since the left-right asymmetry of the depth of the STS develops already *in utero*, with the right STS developing about two weeks earlier (23 vs. 25 gestational weeks) than its counterpart of the left hemisphere (Kasprian, Langs, Brugger *et al.*, 2011). This structural asymmetry remains throughout the entire life span (Glasel, Leroy, Dubois, Hertz-Pannier, Mangin & Dehaene-Lambertz, 2011; Leroy *et al.*, 2015), but its functional consequence remains unclear. So far, no direct relation to the functional asymmetry of speech and language functions have yet been reported (Leroy *et al.*, 2015; Specht, 2014).

#### Functional neuroanatomy of the STS

The functional neuroanatomy of the STS indicates – so far – its involvement in speech perception, Audiovisual Integration (AVI),

theory of mind (ToM), face perception, face-voice integration, and perception of biological motion (Beauchamp, 2015; Deen, Koldewyn, Kanwisher & Saxe, 2015; Hein & Knight, 2008; Vander Wyk, Voos & Pelphrey, 2012; Watson, Latinus, Noguchi, Garrod, Crabbe & Belin, 2014). Interestingly, most reported functions can be linked to social cognition (Deen *et al.*, 2015). In the following, three of these functions will be discussed in more details.

#### Speech perception

As already outlined above, neuroimaging studies have consistently demonstrated a strong involvement of lateral parts of the left and right temporal lobe in speech processing (Binder, Frost, Hammeke, Rao & Cox, 1996; Binder, Frost, Hammeke *et al.*, 2000; 2011; Osnes *et al.*, 2011a; Price, 2010, 2012; Scott, McGettigan & Eisner, 2009; Specht, 2013, 2014). Besides the primary auditory cortex and secondary auditory cortex in the posterior third of the STG, functional imaging studies have demonstrated increased activation to phonological cues, phonemes, words, and sentences along a posterior-anterior axis within the temporal lobe, in particular in the left hemisphere. This processing stream has also been labelled as the *ventral stream* for speech perception (Hickok & Poeppel, 2007; McGettigan & Scott, 2012; Specht, 2013, 2014). Within this ventral stream, the STS seems to play a major role in processing mainly phonological signals (Liebenthal, Binder, Spitzer, Possing & Medler, 2005; Price, 2012; Specht, 2014; Specht *et al.*, 2009b; Specht & Reul, 2003). Interestingly, while the left STS and the left ventral stream are most often reported in connection with phonological processing, as demonstrated for example by the “sound-morphing” paradigm (Osnes *et al.*, 2011b; Specht *et al.*, 2005; 2009b), the right STS has been implicated to being crucial for voice perception and prosody processing (Latinus & Belin, 2011; Sammler, Grosbras, Anwender, Bestelmeyer & Belin, 2015). It should be nevertheless be mentioned, that current models of speech perception also include several other areas of both hemispheres. Some of these promote a mainly left-hemispheric dorsal and ventral pathway for speech perception

(Hickok & Poeppel, 2007), with a more right-hemispheric network for prosody processing (Sammler *et al.*, 2015), but some promote a triple-stream model combining all these aspects (Specht, 2014).

### Audiovisual integration

There is substantial evidence for an involvement of the STS in multisensory processing. Imaging studies have repeatedly demonstrated that certain auditory and visual processes activate overlapping areas within the STS, with several studies specifically linking the posterior STS (pSTS) with crossmodal binding of auditory and visual stimuli (Beauchamp, Lee, Argall & Martin, 2004; Calvert, Hansen, Iversen & Brammer, 2001; Nösselt, Bergmann, Heinze, Münte & Spence, 2012; Nösselt, Rieger, W., Schoenfeld *et al.*, 2007; Stevenson, Geoghegan & James, 2007; Uno, Kawai, Sakai *et al.*, 2015). In connection with speech perception, this structure has been identified as being central in detecting audio-visual incongruences, such as the McGurk effect, (Nath & Beauchamp, 2012; Saito, 2005; Szycik, Stadler, Tempelmann & Münte, 2012), but also voice perception in general (Alho, Vorobyev, Medvedev *et al.*, 2006; Belin, Zatorre, Lafaille, Ahad & Pike, 2000; Campanella & Belin, 2007). With respect to the McGurk effect, lip reading can be viewed as a form of biological motion perception, which is yet another function of the posterior STS (Flack, Andrews, Hymers *et al.*, 2015; Han, Bi, Chen, Chen, He & Caramazza, 2013; Herrington, Nymberg & Schultz, 2011; Puce & Perrett, 2003; Sokolov, Erb, Gharabaghi, Grodd, Tatagiba & Pavlova, 2012; Vander Wyk *et al.*, 2012). This can further be related to social cognition and theory of mind processes (Beauchamp, 2015).

### Theory of mind

Theory of mind (ToM) refers to the ability to attribute mental states to others, or broken down more clearly, to assume the viewpoint of others, to imagine what they perceive, to infer the intention of an observed action, and to interpret observed interactions between different subjects (Frith & Frith, 2003; Gallagher & Frith, 2003). The traditional approach to assess ToM abilities is with short stories or animated cartoons, describing or displaying situations and interactions that require the reader (the subject) to infer mental states to others (in this case the cartoon figures) (Hein & Knight, 2008). Imaging studies have consistently identified in particular the right posterior superior and middle temporal cortical areas as being involved in ToM processes, accompanied by parietal and medial and inferior frontal areas (Brunet, Sarfati, Hardy-Baylé & Decety, 2000; Dodell-Feder, Koster-Hale, Bedny & Saxe, 2011; Fletcher, Happel, Frith *et al.*, 1995; Goel, 2007; Laurita, Hazan & Spreng, 2017; Tettamanti, Vaghi, Bara, Cappa, Enrici & Adenzato, 2017; Völlm, Taylor, Richardson *et al.*, 2006). Accordingly, within this “mentalizing network,” deviations have been observed in multiple conditions associated with mentalizing difficulties, including schizophrenia (Brunet, Sarfati, Hardy-Baylé & Decety, 2003; Sugranyes, Kyriakopoulos, Corrigall, Taylor & Frangou, 2011; Völlm *et al.*, 2006; White, Frith, Rellecke, Al-Noor & Gilbert, 2014) and autism (Baron-Cohen, Ring, Wheelwright *et al.*, 1999; Castelli,

Frith, Happel & Frith, 2002; Greimel, Nehrkorn, Schulte-Rüther *et al.*, 2012; Sugranyes *et al.*, 2011)

Taken together, it is evident that the STS is a highly multifunctional cortical region, but the degree of functional differentiation and the anatomical overlap of different functions remains unclear. Considering the brief aforementioned (and by far incomplete) review of findings, it is arguable that there is some anatomical subdivision and functional differentiation between the left and right STS and the posterior and middle part of the STS, while reports about the anterior part of STS are more sparse (see also Deen *et al.*, 2015, for a more differentiated division of the STS). And though evidence points to a bilateral involvement of the STS region, data nonetheless indicates a left lateralised functional specialisation for speech perception, and a right lateralised functional specialisation for theory of mind abilities as well as voice and face perception (Deen *et al.*, 2015). There is, however, an ongoing discussion whether the STS is multifunctional, but dependent, on higher-order brain regions (Hein & Knight, 2008), or whether the STS shows a functional heterogeneity with separable functional specialisations (Deen *et al.*, 2015). The posterior and middle part of STS are in particular the focus of this discussion.

Given the unconcluded discussion on the multifunctionality of the STS, the present study aims to explore the differentiation and lateralisation of the posterior and middle part of the STS by applying a within-subject fMRI design to investigate and identify neuronal activation within the STS in response to speech perception, audiovisual integration, and theory of mind, as well as their functional connectivity, asymmetry, and possible relations to the structural asymmetry of the STS.

## MATERIAL AND METHODS

### Participants

The participants were 20, right-handed, healthy male adults. For technical reasons two participants were excluded from all subsequent analyses, and one additional participant from the structural analysis only. The remaining 18 participants were between 21–29 years old (mean 25.7  $\pm$  2.5). Participants were recruited from the student population at the University of Bergen and the local hospital (Haukeland University hospital) staff population. Handedness was determined by a modified version of the Edinburgh Inventory (Oldfield, 1971), which contained in total 15 questions, including the original questions of the Edinburgh Inventory and some additional everyday tools. Questions could be scored as “mainly left,” “mainly right,” or “both hands.” All participants were right-handed (averaged score 14.3  $\pm$  1.3 of maximal 15 items). All participants gave written informed consent in accordance with the Declaration of Helsinki and local institutional guidelines. The regional ethics committee of the State Department of Health (REK) approved the study.

### Paradigms and stimuli

Each participant performed three different tasks, or paradigms, which should activate the posterior and middle parts of the STS: Speech perception, audiovisual integration, and theory of mind. The paradigms were separated into three runs, but within the same scanning session, and the order of the three runs was manually randomized across the participants.

**Speech perception.** To investigate the neuronal activation associated with speech perception, the study employed the previously described sound-morphing paradigm (Osnes *et al.*, 2011b, 2011a; Specht *et al.*, 2005;



2009b). This paradigm was chosen since it has proven to be an effective paradigm in showing a strong functional asymmetry within the STS (Specht, 2013, 2014; Specht *et al.*, 2009b). A detailed description of the stimuli can be found in Specht *et al.* (2009b). In short, participants were presented with morphed consonant-vowels (CV) /da/ and /ta/ as speech stimuli, and guitar sound (A3) and a piano chord (C major triad on a C3 root) as control stimuli. Further, white noise served as common starting point for all morphing procedures, and was matched in duration and mean intensity to the speech and non-speech stimuli. The stimuli material was further manipulated by creating a parametric transition from white noise into either speech or non-speech sounds. This resulted in seven separate stimuli that, if played in the correct order, would for instance correspond to a sound “morphing” from white noise into a CV syllable. However, to avoid expectation effects, that is, anticipating that a sound shall morph into a speech sound (Osnes, Hugdahl, Hjelmervik & Specht, 2012), the stimuli were never played in a consecutive order but were pseudorandomized across all factors. The subsequent analyses differentiated only between speech and non-speech, that is, not between the underlying stimuli themselves (e.g., between /da/ and /ta/ or between the piano and guitar sound). In the present design, each stimulus category and manipulation step had 14 repetitions. This paradigm included in total 182 regular events and 86 null events (i.e., trials with no stimuli). To keep attention constant during fMRI data acquisition, an unrelated behavioural task was included in which participants were instructed to report with a response button, placed in the dominant hand, whenever they heard a stimulus in only one ear. The design included 14 target trials which were randomly distributed, with an equal number of trials for the left and right ear, respectively. In the subsequent analysis, only the effect of the parametric modulation of the speech sounds was used for the group analysis, since earlier studies have demonstrated a strong functional asymmetry within STS for this contrast (Osnes *et al.*, 2011b, 2011a; Specht *et al.*, 2009b).

**Audiovisual Integration (AVI).** The AVI condition included three separate tasks: a simple audiovisual integration task, a visual control task, and an auditory control task. The audiovisual integration task consisted of showing the participants a blank black screen in which a white asterisk would appear, either synchronous or dis-synchronous with a simple short-pitched sine-wave tone (1000 Hz) being played into both ears. Participants were instructed to indicate with a single response button (placed in the right hand) whether the asterisk and the tone appeared *not* synchronous. In the visual control task, participants were only shown the blank black screen with appearing white or grey asterisks and were instructed to indicate with the response button if an appearing asterisk was gray. In the auditory control task, participants heard the same single short-pitched tone, on either both or one of their ears, and they were instructed to respond with the response button if they heard the tone only in one ear. During the auditory control task the visual stimuli-screen was left blank. There were six blocks for the integration task and three blocks each for the visual and auditory control tasks. Each block contained 15 trials, with each trial lasting on average 2.2 seconds. The three tasks were presented in a fixed intermittent sequence, and with an instruction on how to respond before each block. In the subsequent analysis, only the difference in contrast between the AVI task and the two control conditions was used for the group analysis.

**Theory of mind.** To explore theory of mind processes the study used comic strip cartoons adapted from Brunet *et al.* (2000, 2003). This paradigm included an experimental ToM task and a control task. The experimental setup of the ToM condition (task) included 28 ToM cartoon stories, where each story consisted of three cartoons, displayed in the upper half of the screen and to be read from left to right. Each cartoons showed a person performing an everyday action. In the lower left and right corner there were displayed two additional cartoons, of which only one of them would be a logical continuation of the action, and participants had to indicate by pressing the response button whether the left or right cartoon was the correct one. To solve this task correctly, participants have to infer on the intention of the displayed action, since the alternative cartoons were also possible actions but not related to the story. The

participants were given one response button in each hand for indicating their choice.

The control condition had the same setup, but the cartoons here were not telling a story and two cartoons were displayed twice in the top row. In the lower row the repeated cartoon, as well as an additional cartoon, was presented and participants had to indicate which of the two was displayed twice in the upper row. This task therefore does not require the participant to infer intention.

A block design was used for the ToM paradigm, comprising six blocks per condition, with seven trials each, supplemented with six blocks without any stimulation. The order of the blocks was pseudorandomised. Within each block, trials were presented in a randomized order, with each trial presented for 4.5 seconds. In the subsequent analysis, only the difference contrast between the ToM task and the control condition was used for the group analysis.

### Experimental procedure

Auditory stimuli were presented through MR-compatible headphones with insulating materials that also compensated for the ambient scanner noise by 24 dB. Visual stimuli were presented through MR-compatible goggles, which were mounted to the head coil. Presentation of the visual and auditory stimuli, and also the recording of the behavioural responses, was controlled by the E-prime software (E-Prime 2 Professional, Psychology Software Tools Inc., Sharpsburg, PA). The order of the three paradigms was intermixed, such that one-third of participants started with the ToM, one-third with the AVI, and one-third with the SM paradigm.

### Data acquisition

The fMRI study was performed on a 3-T GE Signa Exite scanner. The scanning protocol consisted of a high-resolution T1-weighted structural imaging, three fMRI runs, and a diffusion tensor imaging (DTI) sequence. The axial slices for the functional imaging, based on an EPI sequence, were positioned parallel to the AC–PC line with reference to the structural image. The functional images were acquired with an EPI sequence, with the following parameter: 25 axial slices (64 × 64 matrix, 3 × 3 × 5.5 mm voxel size, TE 30 ms, TR 1500ms) that covered the cerebrum and most of the cerebellum. 285 EPI volumes were acquired for the SM paradigm, with a 2.3s silent gap after each volume for stimulus presentation, resulting in an effective TR of 3.8s; 432 EPI volumes were acquired for the AVI paradigm, with no silent gap; and 360 EPI volumes were acquired for the ToM paradigm, with no silent gap. The first three volumes for each paradigm were treated as dummy scans and removed prior to the subsequent processing.

### Data analysis

**fMRI Data pre-processing.** The BOLD-fMRI data were pre-processed and statistically analysed with SPM12 (<http://www.fil.ion.ucl.ac.uk/spm>). The EPI images were first re-aligned to adjust for head movements during the image acquisition and the images were corrected for movement-induced distortions (“unwarping”). Data were subsequently inspected for residual movement artefacts. The realigned image series were then normalized to the stereotaxic Montreal Neurological Institute (MNI) reference space, provided by the SPM12 software package (using “Old Normalization”), and resampled with a voxel size of 2 × 2 × 2 mm. The images were then finally smoothed using a Gaussian kernel of 8 mm.

**fMRI data analysis.** On the first level, the three paradigms were analysed separately by specifying a general linear model (GLM) that contained the regressors for the respective conditions and the realignment parameter as covariates of no interest.

Group effects for the paradigms were analysed in three separated one-sample *t*-tests. In addition, a global conjunction analysis across the three paradigms was created through a one-way ANOVA model. A global conjunction, that is, a minimal *t*-statistic, was selected in order to detect areas that show the same trend in all conditions without the requirement of

being significant in each of the three conditions (Friston, Holmes, Price, Büchel & Worsley, 1999; Friston, Penny & Glaser, 2005).

All analyses were explored with a family-wise error (FWE) corrected threshold of  $p < 0.05$ , together with a cluster threshold of at least 10 voxels per cluster.

### Functional & Structural Asymmetry

A region of interest (ROI) analysis was performed by extracting the averaged, task-positive BOLD signals from 8mm spheres, which were placed in the posterior, middle, and anterior STS (see Table 1 for the coordinates). Laterality indices were estimated for each region and each task, using the formula:  $LI = 100 \times (L-R)/(L+R)$ , with L = activation of left STS and R = activation of right STS.

The structural data were segmented by the semi-automated segmentation, normalization, and anatomical labelling procedure, as included in BrainVisa (www.brainvisa.info). In the subsequent analyses of left-right asymmetries, measures of the length, maximal and mean depth of the STS were used.

## RESULTS

### GLM

The parametric modulation of the speech sounds caused a correlated change in brain activation within the left and right middle part of the superior temporal sulcus (see red areas in Fig. 2a, Table 1). Note, this contrast only displays the response to the parametric

manipulation and not the response to the auditory perception per se, which was not explored in the context of this study.

When the activations from the pure sensory-control conditions are subtracted, the audiovisual integration task resulted in bilateral activation of deeper areas of the STS and auditory cortex, not overlapping with those from the sound-morphing condition (see blue areas in Fig. 2a, Table 1).

Lastly, the ToM task resulted in widespread activations comprising the posterior temporal lobe, inferior parietal, frontal, and occipital areas (see green areas in Fig. 2a, Table 1). Of relevance for the current study, the activations in the left and right posterior STS did not overlap with the activations from any of the other conditions

### Conjunction

The conjunction analysis revealed three areas that shared consistent activations, according to a minimum t-statistic. These were the posterior STS (pSTS) of the right and left hemisphere, and the left middle STS (see Fig. 2b, Table 1).

### Functional Asymmetry

The analyses of functional asymmetries revealed no significant asymmetries of the AVI and ToM task within the STS (all  $p > 0.1$ ).

Table 1. Description of brain activations in terms of anatomical localisation, MNI coordinates, and statistics for the peak voxel and cluster size (number of voxels per cluster, voxel size  $2 \times 2 \times 2$ mm); few = family-wise error correction.

Anatomy					peak		cluster	
Area	Side	x	y	z	T	p(FWE)	#voxel	p(FWE)
Audiovisual Integration								
mSTS	Right	52	-18	0	8.32	0.005	107	<0.001
mSTS/HG	Left	-38	-32	6	7.18	0.021	20	0.007
Sound morphing								
mSTS	Left	-60	-22	8	10.78	<0.001	86	<0.001
mSTS	Right	64	-10	-6	9.08	0.002	116	<0.001
Theory of mind								
pSTS, ANG, SMG, STS, MTG	Left	-48	-62	14	18.43	<0.001	4501	<0.001
IFGtri, IFGop, MFG	Left	-46	24	10	11.94	<0.001	2590	<0.001
MFG, PrCG	Right	46	6	46	11.06	<0.001	147	<0.001
pSTS, ANG, SMG, STS, MTG	Right	48	-66	16	10.84	<0.001	1471	<0.001
IFGtri, IFGop, MFG	Right	46	20	26	10.74	<0.001	275	<0.001
SFG	Left	-10	44	52	9.01	0.001	46	<0.001
FG	Right	30	-40	-18	8.99	0.001	137	<0.001
SMA	Left	-6	18	50	8.85	0.002	110	<0.001
IFGor	Right	34	28	-18	7.68	0.009	46	<0.001
IOG, MOG	Right	36	-92	12	7.60	0.010	12	0.007
IFGor	Left	-46	36	-6	7.35	0.015	22	0.002
SFG	Left	-14	24	64	7.20	0.018	17	0.004
Cerebellum	Left	-16	-78	-32	7.07	0.022	14	0.005
Cerebellum	Right	16	-84	-36	7.06	0.023	17	0.004
Pallidum	Left	-12	2	0	7.06	0.023	10	0.008
Conjunction								
pSTS	Left	-52	40	2	2.97	0.001	26	0.002
pSTS	Right	50	-38	2	2.87	0.002	100	<0.001
mSTS	Left	-50	-22	-10	2.67	0.006	10	0.010

Notes: mSTS = middle STS; pSTS = posterior STS; HG = Heschl's Gyrus; ANG = Angular Gyrus; SMG = Supramarginal Gyrus; STG = Superior Temporal Gyrus; MTG = Middle Temporal Gyrus; IFGtri = Inferior Frontal Gyrus, pars triangularis; IFGop = Inferior Frontal Gyrus, pars opercularis; IFGor = Inferior Frontal Gyrus pars orbitalis; MFG = Middle Frontal Gyrus; SFG = Superior Frontal Gyrus; PrCG = Precentral Gyrus; SMA = Supplementary Motor Area; FG = Fusiform Gyrus; IOG = Inferior Occipital Gyrus; MOG = Middle Occipital Gyrus.

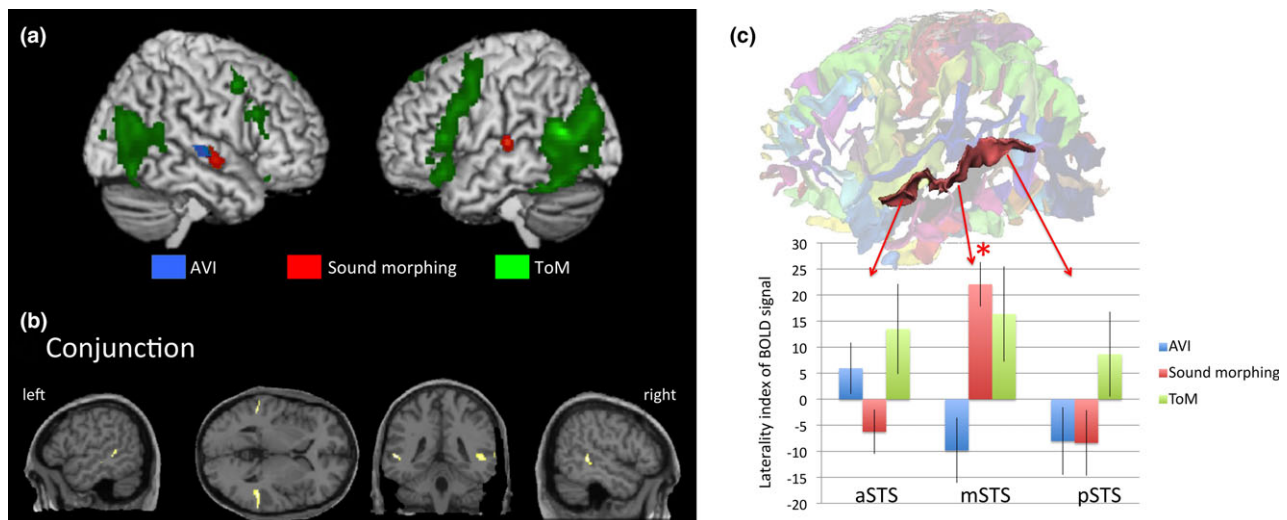


Fig. 2. (a) Brain response to the three conditions (AVI=audiovisual integration; Sound morphing; ToM = theory of mind), when the pure sensory processing has been subtracted (all results  $p$  (FWE)  $< 0.05$ , cluster size at least 10 voxels). (b) Results from the conjunction analysis across the three tasks, using minimal  $t$ -statistics ( $p$ (FWE)  $< 0.05$ , cluster size at least 10 voxels). (c) Analysis of the laterality index of the three conditions. BOLD signals were extracted from the anterior STS (aSTS), middle part of STS (mSTS), and posterior STS (pSTS). Only the sound-morphing condition showed a significant leftward asymmetry in mSTS, as indicated by the asterisk. [Colour figure can be viewed at [wileyonlinelibrary.com](http://wileyonlinelibrary.com)]

However, the sound-morphing paradigm demonstrated a strong leftward asymmetry within the middle part of the STS ( $t(18) = 5.107$ ,  $p < 0.001$ ) (see Fig. 2c).

#### Structural Asymmetry

The maximal depth of the STS of the left hemisphere was  $28.62\text{mm} \pm 2.11\text{mm}$  and of the right hemisphere  $31.40\text{mm} \pm 1.65\text{mm}$ , which was a significant rightward asymmetry ( $t(16) = -5.04$ ,  $p < 0.001$ ). The mean depth of the STS of the left hemisphere was  $17.05\text{mm} \pm 1.27\text{mm}$  and of the right hemisphere  $19.13\text{mm} \pm 1.45\text{mm}$ , which was a significant rightward asymmetry ( $t(16) = -5.391$ ,  $p < 0.001$ ). Finally, the length of the STS of the left hemisphere was  $160.79\text{mm} \pm 24.06\text{mm}$  and of the right hemisphere  $142.23\text{mm} \pm 26.22\text{mm}$ , which gave a moderate leftward asymmetry ( $t(16) = 2.365$ ,  $p < 0.031$ ). Importantly, the asymmetry indices of length were not correlated with those of maximal ( $r = 0.56$ ,  $p = 0.830$ ) and mean depth ( $r = -0.451$ ,  $p = 0.069$ ).

#### Structural – functional correlations

In the final analysis, correlations between the BOLD signal and the structural measures of the STS were performed. These revealed no significant correlations between the length or depth of the STS and the strength of brain activation.

#### DISCUSSION

With this study it was aimed to explore the response of the posterior and middle part of STS activation to three different tasks; audiovisual integration, speech perception, and theory of mind. Moreover, it was aimed to explore the relationship between systematic and reliable structural and functional asymmetries of the STS.

In line with *a priori* hypotheses, all three tasks jointly activated the STS. Of importance, using a stringent family-wise error corrected threshold, none of these activations overlapped, but those from the AVI and sound-morphing condition were adjacent to each other. In addition to the activations observed in the posterior STS, the ToM task mainly activated areas that can be associated with the extrinsic mode network, reflecting cognitive effort and an extrinsically oriented attention while solving the task (Hugdahl, Raichle, Mitra & Specht, 2015).

The results also showed that expected leftward asymmetry for the speech perception task could be replicated (Osnes *et al.*, 2011a; Specht *et al.*, 2009b). By contrast, the audiovisual integration and the ToM task did not show a clear functional asymmetry within the STS. Further, the analysis of structural STS asymmetries confirmed the expected pattern that the STS was longer on the left – but deeper on the right hemisphere. These asymmetries were significant, but did not correlate with each other.

The current study reveals several important findings. First of all, all selected fMRI paradigms jointly activated the superior temporal sulcus, but with a certain spatial distribution, that is, the coordinates of the peak voxels were different between the tasks. Second, all earlier reported asymmetry patterns were replicated, indicating that these are stable and strong asymmetries. On a side note, this also indicates that current study is comprised of a representative sample. Third, the asymmetries in the length and depth of the STS are unrelated and may have different causes. Fourth, the absence of a clear correlation between the STS asymmetry and the fMRI data, strengthens the earlier discussed observation that the STS asymmetry is not directly related to functions such as speech perception.

The importance of these results lies in the fact that this is a within-subject study. Although it has been speculated before, that there is no direct relationship between language functions and the STS asymmetry, the present study can indeed confirm that there



is no direct relationship between any of the anatomical STS asymmetries and the functional asymmetry in phonetic processing. Future studies may also analyse other elements of the language network, such as the modules from dual-stream (Hickok & Poeppel, 2007) or triple-stream (Specht, 2014) models. However, given that the sound-morphing paradigm already generates a stable and replicable asymmetry within the middle part of the STS (see, for example, Specht *et al.*, 2009b), one may predict that other modules of the language network will also not show a relationship with STS asymmetry patterns and functional asymmetry patterns. Nevertheless, the area of the strongest asymmetry during the sound-morphing paradigm closely overlaps with the area of the largest STS asymmetry, called the Superior Temporal Asymmetrical Pit (STAP) (Leroy *et al.*, 2015).

A further finding, there was also no correlation between STS asymmetry patterns and brain activity during the other two tasks. Given the fact that the STS is as stated a core area of the mentalizing network (White *et al.*, 2014), and that the STS is deeply involved in theory of mind tasks and social cognition, one could have speculated a connection between the human-specific asymmetry and related brain functions. On the other hand, ToM tasks are typically not strongly asymmetric, as confirmed by the present study.

With respect to the anatomical measures of the STS, it is important to note that the length and depth of the STS were not correlated with each other, nor were the resulting laterality indices correlated with each other. This may indicate that there is a double dissociation between the factors that cause the development of the asymmetries in length and the asymmetry of depth.

One parameter that has not been explored by this study is the frequency of sulcal pits and *plis de passage* (Im *et al.*, 2010; Leroy *et al.*, 2015; Ochiai *et al.*, 2004). These measures show an asymmetry as well. The sulcal pits appear to be more frequent in the left STS, and the *plis de passage* are more prominent within the left STS, i.e. reaching more often the surface of the left than right STS. It has been speculated that this asymmetry might be related to language functions (Im *et al.*, 2010), and this should be addressed in future studies.

Finally, one may want to speculate on whether the degree of structural asymmetry and the degree of functional asymmetry during speech perception is mediated by the corpus callosum. Earlier studies have shown that the corpus callosum is a modulating factor in dichotic listening performance in adults (Westerhausen, Grüner, Specht & Hugdahl, 2009), and during child development (Westerhausen, Lüders, Specht *et al.*, 2011). However, this aspect still remains unresolved and has to be addressed by future studies.

In conclusion, this study provided further evidence for the multi-sensory and multi-functional organisation of the STS. It further confirmed the marked structural asymmetries of the STS, by showing that the STS is deeper on the right and longer on the left hemisphere. However, this study could not provide evidence of a structural-functional relationship of this asymmetry, as it neither correlated with brain activation during auditory-visual integration, phonological processing, or ToM tasks within the STS nor at any remote areas in the brain. In this respect, this study could indirectly confirm that the asymmetry of the language network is most likely not the cause of this structural asymmetry.

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